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ORIGINAL PAPER

Effects of cover cropping, solarization, and soil fumigation on nematode communities

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Abstract Impacts of sustainable soil-borne pest management strategies on the soil ecosystem were compared to that of methyl bromide fumigation using nematode community analysis. A field experiment was conducted in 2003 and repeated in 2004. Soil treatments carried out in summer months included methyl bromide (MB) fumigation, solarization (S) for 6 weeks, cowpea (*Vigna unguiculata*) cover cropping for 3 months (CP), combination of solarization and cowpea cover cropping (S + CP), and a weedy fallow throughout the summer used as a control (C). All treated plots were planted to pepper (*Capsicum annuum*) after the application of the treatments at the end of the summer. In general, responses of nematode communities to soil treatments were more obvious at pepper planting than at 4 months after planting. In 2003, initial population densities of bacterivores and fungivores at pepper planting followed a hypothesized pattern of MB > S > S + CP > CP > C. However, this perturbation did not persist after a cycle of vigorous growth of a pepper crop. Omnivorous nematodes were the most sensitive nematode trophic group, with impact from soil treatment lasting until the end of the pepper crop. Nematode community indices such as ratio of fungivores to fungivores plus bacterivores, richness, and structure index were especially useful in detecting impacts by the various soil treatments. While disturbance from MB on the nematode communities lasted at least until the end of the pepper crop, that from the solarization often reduced or disappeared at the end of the experiment. The CP treatment enhanced many of the beneficial nematodes but failed to suppress the final population densities of herbivorous nematodes at pepper harvest (Pf). However, CP + S consistently reduced the Pf of herbivores to levels equivalent to MB in both years, whereas, this level of suppression could not be achieved by either CP or solarization alone.

Keywords Cover crop · Integrated management · Methyl bromide alternatives · Nematode ecology · Solarization · Structure index

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Introduction

Knowing that a powerful biocide like methyl bromide (MB) is being removed from the market, scientists are working collaboratively to develop alternative management practices that can suppress multiple soil-borne pests including weeds, plant-parasitic fungi, bacteria, and nematodes. While the negative impact of methyl bromide on the atmosphere is well recognized (Farman et al. 1985; Newman et al. 2004; Rosskopf et al. 2005), and its disturbance to soil ecosystem has been documented (Yeates et al. 1991), limited documentation is available on comparing alternative soil-borne pest management practices to methyl bromide fumigation in terms of their impact on soil ecosystems. Soil fumigants such as methyl iodide, 1,3-dichloropropene, or propargyl bromide are suggested as replacements for MB (Rosskopf et al. 2005), but many of these alternative soil fumigants are as devastating to soil ecosystems (Dungan et al. 2003). Management practices that can maintain soil health are becoming increasingly popular (Abawi and Widmer 2000; Wang and McSorley 2005), and non-chemical approaches as alternatives to methyl bromide are being widely pursued (Obenauf 2004). Whether or not these alternative strategies pose fewer impacts than methyl bromide treatments to the soil ecosystem is important in understanding their short- and long-term effect on soil health.

As suggested by Bongers and Ferris (1999), Ferris et al. (2001), Neher (2001), and Neher et al. (2005), we are using soil nematodes as soil health bioindicators to evaluate several non-chemical alternatives to MB. Freckman and Ettema (1993) demonstrated that human intervention interferes with the nematode fauna. Yeates et al. (1991) compared several parameters for soil biological activities and concluded that abundance and diversity of protozoa and nematodes provide a moderate-term indication of recovery after a major disturbance, better than other parameters such as microbial biomass, bacterial numbers, fungal hyphal length, and N mineralization. Soil nematodes are good soil health bioindicators because they are ubiquitous and have diverse feeding behaviors and life strategies, ranging from colonizer to persister. Some nematodes can survive harsh, polluted, or disturbed environments better than others, and some have short life cycles and respond to environmental changes rapidly (Blakely et al. 2002; Korthals et al. 1998). In general, nematodes are easy to sample and extract from soil, their morphology reflects feeding behavior allowing easy functional classification, and nematode taxa are well classified (Bongers and Bongers 1998; Neher 2001). Through nematode faunal analysis, one can obtain insight into soil food web conditions (Ferris et al. 2001).

One of the more effective non-chemical strategies against several soil-borne diseases and pests is soil solarization (Katan 1987; McGovern and McSorley 1997; Stapleton 2000). This technique relies on solar energy, which is conveyed into soil by covering it with transparent polyethylene for more than 4 weeks. The topsoil layers under the plastic increase in temperature causing mortality of a variety of plant pathogens (Katan et al. 1976). The method has been used successfully against nematode pests in various regions in the world where relatively cloudless and hot weather is available (Greco and Di Vito 2005; Heald and Robinson 1987; Katan 1981; Stapleton and Devay 1983). It has also been effective in regions with humid climates, such as Florida (Chellemi et al. 1993, 1997; McGovern et al. 2004; McSorley and Parrado, 1986), except when prolonged periods of cool rainy weather have occurred (Wang et al. 2004). In addition, solarization can also suppress plant-parasitic nematodes in the summer of temperate regions, such as Oregon (Pinkerton et al. 2000). Information on impact of solarization on the entire nematode community is scarce. Stapleton and DeVay (1983) documented that solarization reduced total abundance of plant-parasitic and free-living nematodes compared to a non-treated control at termination of solarization. Later, Stapleton (2000) speculated that free-living nematodes are more likely to survive solarization, or to colonize rapidly after solarization compared to the plant-parasitic nematodes, providing a healthier environment for plant productivity.

The use of cruciferous residues as soil amendments has been shown to enhance the performance of solarization against soil pathogens (Coelho et al. 2001; Gamliel and Stapleton 1993) and nematodes (Ploeg and Stapleton 2001). Little is known about the effect of integrating a nematode-suppressive leguminous cover crop with solarization, which is a feasible and not excessively costly nematode management practice in Florida. Incorporating a leguminous cover crop into soil can also serve as a green manure to increase soil fertility. In addition, adding organic amendment to soil was found to reduce impact from soil fumigation with 1,3-dichloropropene and propargyl bromide (Dungan et al. 2003). In this study we combined solarization and a cover crop of ‘Iron Clay’ cowpea [*Vigna unguiculata* (L.) Walp.], which is known to be suppressive to the root-knot nematode, *Meloidogyne incognita* (Kofoid & White) Chitwood (Wang et al. 2003a). It is possible that integrating solarization with a leguminous cover crop may improve the suppression of plant-parasitic nematodes and may even reduce any adverse impact from solarization on the overall soil health.

The impact of methyl bromide fumigant on nematode communities in 30 cm-diameter soil cores buried in a field was dependent on site and environmental factors (Yeates et al. 1991). The current study extends the evaluation of impact of methyl bromide to a larger scale, simulating commercial application to field plots with a subsequent crop cycle, as well as comparing methyl bromide fumigation to alternative soil management practices.

The overall objectives of this research were to determine the effects of several pre-plant soil treatments on plant-parasitic nematodes as well as other members of the soil nematode community, with emphasis on impact of soil treatments on the nematode community. We hypothesized that impact of soil treatments on nematode communities would follow a trend of methyl bromide > solarization > solarization + cover cropping > cover cropping > fallow, in which amendment with leguminous cover crop residues should enhance free-living nematodes involved in nutrient cycling but still cause some changes due to cultivation, whereas methyl bromide fumigation and soil solarization would have negative impact (perturbation) on nematode communities based on nematode fauna analysis (Ferris et al. 2001).

Materials and methods

Field experiments were conducted in the 2003 and 2004 fall seasons at the University of Florida Plant Science Research Center, near Citra, Marion County, Florida. The site was previously fallow with native weeds dominated by bahiagrass (*Paspalum notatum* Fluegge) and lambsquarter (*Chenopodium album* L.). The soil was a Candler sand (hyperthermic, uncoated, Entisol) consisting of 95.2% sand, 1.5% silt, and 3.3% clay, with organic matter content of 1.64%.

2003 experiment

On 13 November 2002, 6 months prior to the beginning of the experiment, ‘Dixie’ crimson clover (*Trifolium incarnatum* L.) was sown at a rate of 16.5 kg ha^{-1}. Nitragin® inoculant (Liphatech Inc., Milwaukee, WI), consisting of *Rhizobium leguminosarum* bv *trifolii* in peat base (99 g) was added to the crimson clover seed (99 g inoculant per 45 kg seed) to improve its nitrogen-fixing capability. Crimson clover biomass was disked and plowed under on 28 April 2003. Five soil treatments were applied: methyl bromide (MB), solarization (S), cowpea (CP), cowpea + solarization (CP + S), and weedy fallow control (C). Treatments were arranged in a randomized complete block design with 6 replications (a total of 30 plots). Each plot was 2.43 × 18.24 m.

‘Iron Clay’ cowpea was planted as a summer cover crop in plots designated for CP and S + CP treatments at a rate of 56 kg ha^{-1} on 2 May 2003. During this period, plots without cowpea treatment were left fallow with weeds. The cowpea was irrigated by an overhead sprinkler system as needed. Cowpea biomass was plowed under on 7 July 2003, and cowpea plots were rototilled a total of 6 times before the solarization treatment.

Solarization was initiated on 8 July 2003 in S and S + CP plots by rototilling the soil prior to establishing planting beds of 0.9 m wide × 18.24 m long × 20-cm high. Planting beds were then covered with a transparent, 25-μm-thick, uv-stabilized, low-density polyethylene mulch (ISO Poly Films, Inc., Gray Court, SC). Soil moisture content prior to bed formation for solarization averaged 6%. Soil temperatures were monitored at 5 and 15 cm soil depths in S, S + CP, and C using WatchDog dataloggers (Spectrum Technologies, Inc., Plainfield, IL) throughout the solarization period, which lasted 6 weeks until 18 August. During this period, non-solarized plots were left fallow. Weeds heavily colonized plots designated to receive MB and C treatments.

On 13 August, MB, C, and CP plots were rototilled to remove weeds. All beds were reformed or formed on 20 August, drip irrigation lines were installed and beds were covered with silver reflective mulch (Sonoco Agricultural Films, Hartsville, SC). MB fumigated plots received an application of 448 kg ha^{-1} of 67% methyl bromide + 33% chloropicrin and were covered by plastic mulch.

'Wizard X3R' bell pepper (*Capsicum annuum* L., a good host of root-knot nematode) seedlings (7–10 cm tall) were transplanted on 9 September into double rows in each bed with distance of 30.5 cm between rows and 45.7 cm between plants in a row, for a total of 75 plants per plot. A number of seedlings (< 5%) were replaced due to cutworm damage. Peppers were irrigated as needed and fertilized through the irrigation system with 3.36 kg N ha^{-1} per day, 5 days per week for the entire crop (3 months), for a total of 202 kg N ha^{-1}. Plants were protectively sprayed with maneb, mancozeb, and copper hydroxide to prevent foliar fungal diseases and bacterial leaf spot [*Xanthomonas campestris* pv. v*esicatoria* (Doidge) Dye]. Peppers were harvested three times between 18 November and 9 December.

Soil samples were collected from each plot after MB treatment, but before pepper planting (9 September = Pi), and at the end of the pepper crop (9 January 2004 = Pf). Six soil cores (2.5 cm diameter × 20 cm deep) were taken from each plot and combined into one composite sample. Nematodes were extracted from a 100-cm^3 subsample by a modified sieving and centrifugal flotation method (Jenkins 1964).

2004 experiment

The test was repeated at the same site in the following summer, with all treatments remaining in the same plots as in 2003. Protocol was similar to that described for the 2003 experiment, with some minor modifications specified as follows. Cowpea was planted on 28 April 2004. Weeds in plots that did not receive the CP treatment were sprayed with glyphosate (a.i. 4.67 kg ha^{-1}) on 21 June. The cowpea cover crop was plowed under on 29 June. The solarization treatment was initiated on 30 June after rototilling and terminated on 17 August. Weeds in MB and C treatments were managed with glyphosate again on 4 August. The MB treatment was applied on 17 August. Pepper seedlings were transplanted on 31 August.

A major difference between the 2003 and 2004 tests was the active hurricane season in 2004, resulting in flooding and a soil-borne disease epidemic (Saha et al. 2005). Hurricanes Frances (5, 6 September) and Jeanne (26 September) struck this site and produced 406 mm and 36 mm of rainfall, respectively. Although high pepper plant mortality rates were recorded, the experiment proceeded through pepper harvest from 30 November to 14 December 2004. Soil samples were collected on 29 August (Pi) and 14 December (Pf), and extracted for nematodes as described earlier.

Nematode assay

In both experiments, nematodes were usually identified to genus (but occasionally to family or order), counted, and assigned to one of five trophic groups: bacterivores, fungivores, herbivores, omnivores, or predators (Yeates et al. 1993). The feeding habit of Tylenchidae (*Filenchus* and *Tylenchus*, with some *Ditylenchus*) was classified as fungivore. Yeates et al. (1993) had classified these genera as plant associates or fungivores based on literature from Linford (1937) and Wood (1973). The importance of fungivory in this group is confirmed by recent studies on population growth rates of *Filenchus* on different isolates of fungal culture (Okada and Kadota 2003; Okada et al. 2005), and by increased abundance of these nematodes in potted soil amended with crop residues without the presence of plants (McSorley and Frederick, 1999). *Monhystera* was grouped as a bacterivore rather than a substrate ingestor (Yeates et al. 1993). The total number and the percentage of every trophic group in the community were calculated. Nematode richness was the total number of taxa recorded per sample.

The fungivore to fungivore plus bacterivore (F/F + B) ratio was calculated to characterize decomposition and mineralization pathways (Freckman and Ettema 1993). The nematode fauna was also analyzed by a weighted system for nematode functional guilds in relation to structure of the food web (Ferris et al. 2001). The structure index (SI) reflects the degree of trophic connection in food webs of increasing complexity as the system matures, or progressive food web simplicity as the system degrades (Ferris et al. 2001). This index was calculated as $SI = 100 \times [s/(s + b)]$ where s and b are the abundance of nematodes in guilds representing structure, and basal food web components, respectively (Ferris et al. 2001). A higher SI indicates a food web that is more structured or stable, with more persisters (k-strategist) genera present.

Statistical analysis

Data were subjected to one-way analysis of variance (ANOVA) using the Statistical Analysis System (SAS Institute, Cary, NC). To ensure that data fit a normal distribution prior to analysis, nematode abundance data were log-transformed by $\log(x + 1)$. However, only untransformed arithmetic means of all data are presented.

Results

Soil temperature

Daily maximum soil temperatures are presented (Fig. 1). In general, S or S + CP had similar temperatures at the same soil depth, and were higher than those in the CP and C treatments. At 5-cm soil depth in 2003, both S and S + CP resulted in 29 days of maximum temperatures ≥42°C. In 2004, the numbers of days with maximum temperature ≥42°C at 5-cm depth was 33 for S + CP and 29 for S. Fewer days achieved this temperature at a deeper soil depth (15-cm) in S and S + CP. In non-solarized plots, most days did not reach temperatures ≥42°C, except for 2 days in the CP treatment in 2004. Data reported in the literature and the results of preliminary laboratory tests indicate that 42.5°C is the minimum soil temperature causing the mortality of damaging herbivore nematodes such as reniform and southern root-knot nematodes (Heald and Robinson 1987; Wang K-H, unpublished).

Impacts on nematode abundance

Impact of pre-plant soil treatments on total abundance of each nematode trophic group in 2003 was similar to our hypothesis that perturbation on nematode communities followed a trend of MB > S > S + CP > CP > C, with greatest numbers of nematodes occurring in the CP and C treatments (Table 1). Total abundance of bacterivores at planting (Pi) of the pepper crop (at the end of the summer) was highest in the C followed by CP ($P \leq 0.05$, Table 1), whereas those in S, S + CP, and MB were less than that in C ($P \leq 0.05$, Table 1). Most bacterivores that were affected by these soil treatments followed a similar trend. Impact of soil treatment on the total abundance of fungivores at Pi was even more pronounced. *Aphelenchoides, Filenchus*, *Tylenchus*, and *Aphelenchus* were the dominant fungivores present. Abundance of fungivores followed the same trend as that of the baterivores, i.e. a trend of C > CP > S, S + CP, and MB. All treatments reduced herbivores ($P \leq 0.05$; Table 1) compared to the control C. The most common herbivore present was *Mesocriconema*; *Meloidogyne* was not detected in this initial sampling. On the other hand, the effect of most soil treatments on numbers of omnivores was not different from the C except for the CP treatment, which increased ($P \leq 0.05$) the abundance of total omnivores as compared to the C. *Aporcelaimellus* and *Eudorylaimus* were the most abundant omnivores. Predatory nematodes were most abundant in C and CP (*Mylodiscus* sp.), as well as S (*Seinura* sp.) ($P \leq 0.05$).

This initial impact on most nematode trophic groups did not persist toward the end of pepper crop in 2003. Final population densities (Pf) of bacterivores were able to recover in all treatments to levels not different from the C (Table 1). Trends in total bacterivore levels were determined primarily by the abundant *Acrobeloides* and Rhabditidae. Final population densities (Pf) of fungivorous nematodes in CP, S, and S + CP

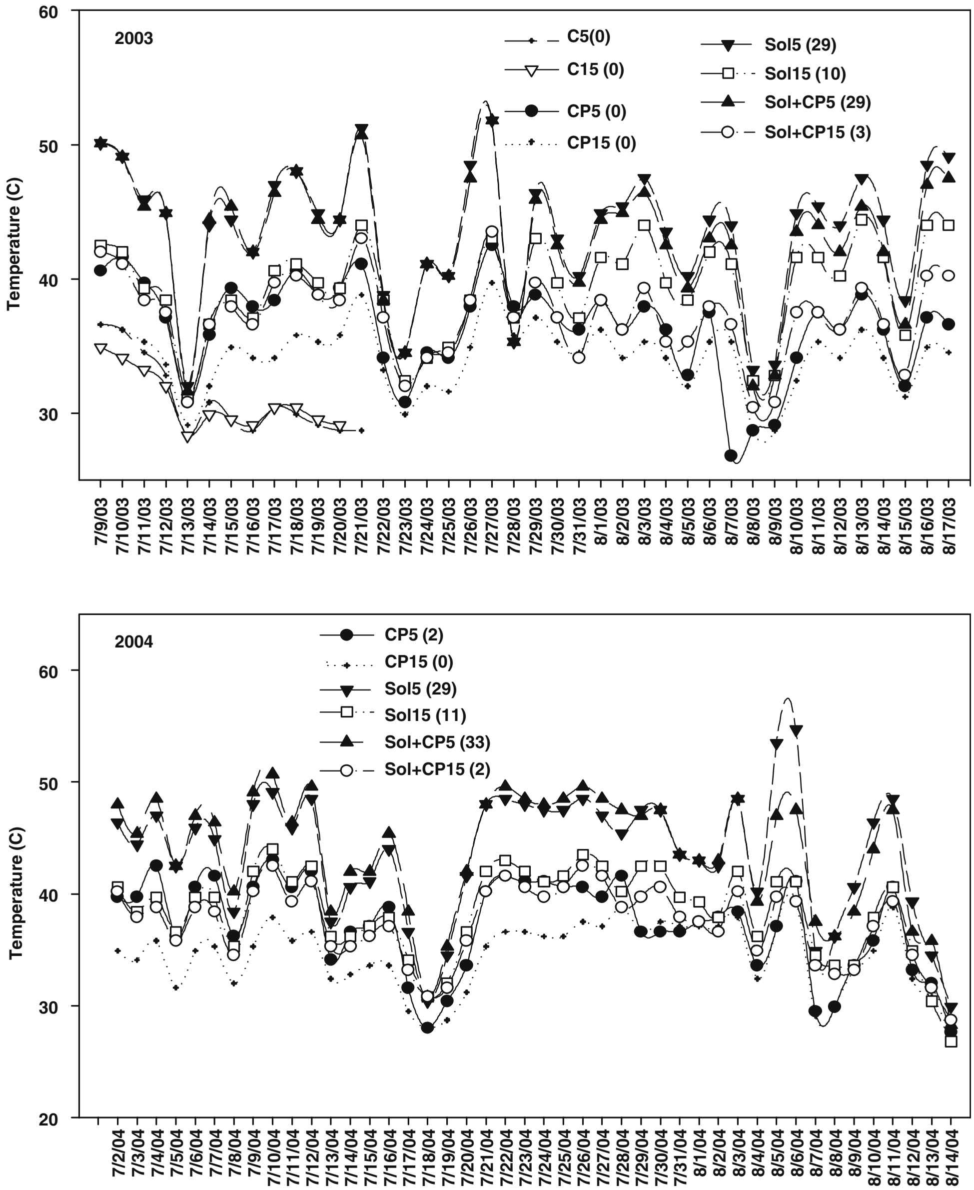

Fig. 1 Maximum daily soil temperature at two soil depths (5 and 15 cm) during the summer solarization periods of 2003 and 2004 experiments. Treatment codes are soil treatment followed by soil depth, where S = solarization, S + CP = solarization + cowpea, CP = cowpea, C = control. Number in parenthesis following the treatment code is the number of days with maximum temperature >42°C throughout the solarization period

treatments were able to recover to levels not different from C, but those in MB remained less than C ($P \leq 0.05$). Among the herbivores, *Meloidogyne* increased at the end of the pepper crop in the non-chemical treatments and was the most dominant herbivore in CP and S treatments (Table 1). Unlike other trophic groups, impact of soil treatments on the abundance of omnivores were more evident at the end of the pepper crop, with omnivore numbers greatest ($P \leq 0.05$) in C and least in MB.

Impact of soil treatments on Pi of most nematode trophic groups in 2004 was slightly different from that in 2003. Abundances of some free-living nematode trophic groups in the C were lower than those observed in 2003, and were as low as

Table 1 Effects of pre-plant soil treatments on abundance of nematodes and other invertebrates at the beginning and end of pepper crop in 2003 Experiment

Nematode taxon	Numbers per 100 cm^3 soil				
	Methyl bromide	Solarization	Solarization + Cowpea	Cowpea	Control
	9 September 2003				
Bacterivores					
Acrobeles	9 c[a]	0 d	12 bc	36 ab	40 a
Acrobeloides	16 b	16 b	28 b	50 ab	122 a
Cephalobus	0 b	42 a	2 ab	0 ab	2 ab
Eucephalobus	16 b	1 c	2 c	11 b	63 a
Rhabditidae	15 bc	65 ab	5 c	65 a	80 a
Zeldia	2 ab	0 b	2 ab	4 a	1 ab
Total	67 c	138 bc	49 c	195 ab	345 a
Fungivores					
Aphelenchoides	3 b	5 b	0 c	7 b	40 a
Aphelenchus	1 c	2 c	2 bc	8 ab	18 a
Filenchus	4 bc	0 d	2 c	10 b	30 a
Tylenchus	1 c	0 c	1 c	7 b	22 a
Total	13 c	8 c	6 c	38 b	106 a
Herbivores					
Mesocriconema	2 b	0 c	5 b	2 b	15 a
Total	6 b	0 c	10 b	5 b	24 a
Omnivores					
Total	3 b	0 c	1 bc	14 a	2 bc
Predators					
Total	0 b	4 a	0 b	6 a	4 a
Total Nematodes	96 c	152 c	68 c	268 ab	509 a
Enchytraeid worms	2 bc	0 c	5 a	7 ab	2 ab
	9 Jan 2004				
Bacterivores					
Acrobeles	23 b	26 ab	32 ab	15 b	64 a
Acrobeloides	583 a	686 ab	324 ab	391 ab	130 b
Rhabditidae	122 a	62 a	107 a	187 a	98 a
Zeldia	55 a	11 b	32 ab	12 b	12 b
Total	801 a	862 a	620 a	696 a	369 a
Fungivore					
Aphelenchoides	4 b	46 a	38 a	46 a	42 a
Aphelenchus	10 ab	2 b	5 ab	7 ab	14 a
Filenchus	33 a	57 a	64 a	27 a	60 a
Total	50 b	114 ab	149 a	88 ab	120 a
Herbivores					
Meloidogyne	2 c	188 ab	44 bc	330 a	21 bc
Total	2 c	192 ab	48 b	330 a	32 b
Omnivores					
Total	0 c	1 bc	2 ab	3 ab	5 a
Predators					
Total	0 a	2 a	0 a	1 a	1 a
Total nematode	854 a	1179 a	824 a	1122 a	533 a
Enchytraeid worms	2 d	4 cd	14 a	7 bc	13 ab

[a]Values are arithmetic means of four replications (not transformed) and are round to whole numbers. Means in a row followed by same letter(s) are not different according to Waller–Duncan k-ratio (k = 100) t-test based on log (x + 1) transformed values

those in the MB or S treatments (Table 2). Abundance of bacterivorous and fungivorous nematodes were greater in CP than in C, S, and MB (Table 2). While the abundance of herbivores, omnivores and predatory nematodes was very low, some minimal impact of soil treatments on these trophic groups occurred.

In 2004, Pf of bacterivorous nematodes in all treated plots were lower than C, unlike the recovery that occurred in 2003 (Table 2). Much of this trend is due to the great abundance of Rhabditidae in C plots at Pf in 2004. The Pf of fungivorous nematodes, however, followed the trend of perturbation, with abundance ranging from C > CP,

Table 2 Effects of pre-plant soil treatments on abundance of nematodes and other invertebrates at the beginning and the end of pepper crop in 2004 Experiment

Nematode taxon	Numbers per 100 cm^3 soil				
	Methyl bromide	Solarization	Solarization + Cowpea	Cowpea	Control
	29 August 2004				
Bacterivores					
Acrobeles	1 c[a]	23 b	24 b	53 a	20 b
Acrobeloides	3 c	4 bc	21 a	26 a	5 b
Prismatolaimus	0 b	1 b	2 b	6 a	7 a
Rhabditidae	13 b	2 b	12 b	92 a	9 b
Zeldia	0 c	1 c	6 b	22 a	7 b
Total	28 c	68 b	126 ab	244 a	92 b
Fungivores					
Aphelenchoides	2 a	6 a	1 a	17 a	1 a
Aphelenchus	1 d	4 c	11 b	42 a	12 b
Filenchus	0 b	2 ab	6 ab	5 a	3 ab
Total	4 c	8 c	25 b	68 a	19 b
Herbivores					
Meloidogyne	0 a	2 a	0 a	0 a	1 a
Total	0 b	10 a	3 ab	1 ab	4 a
Omnivores					
Total	0 b	0.5 ab	2 a	2 a	0 b
Predator					
Total	0 c	0.2 ab	0.5 ab	1 a	0 b
Total nematodes	32 c	86 b	158 ab	316 a	116 b
Enchytraeid worm	0 c	3 b	19 a	8 ab	12 a
	14 December 2004				
Bacterivores					
Acrobeles	6 b	4 b	11 ab	7 ab	33 a
Acrobeloides	61 ab	76 ab	59 ab	45 b	147 a
Prismatolaimus	0 c	4 ab	12 a	2 bc	12 ab
Rhabditidae	14 b	26 b	17 b	13 b	349 a
Zeldia	2 b	3 ab	12 ab	9 ab	12 a
Total	110 b	128 b	155 b	93 b	615 a
Fungivore					
Aphelenchoides	1 c	7 abc	3 bc	13 ab	17 a
Aphelenchus	4 b	10 ab	4 b	10 ab	25 a
Filenchus	1 c	1 c	8 ab	4 b	12 a
Tylenchus	0 ab	0 a	3 ab	0 b	8 a
Total	6 c	19 b	18 b	32 ab	72 a
Herbivores					
Meloidogyne	0 c	78 a	13 bc	49 ab	332 a
Total	0 c	80 a	15 b	50 ab	342 a
Omnivores					
Total	0 a	0 a	1 a	1 a	3 a
Predators					
Total	0 a	0 a	1 a	1 a	0 a
Total nematodes	117 b	229 b	194 b	178 b	1036 a
Miscellaneous					
Meloidogyne infected by *Drechmeria*-like spores	0 c	11 ab	4 bc	8 bc	92 a

[a]Values are arithmetic means of four replications (not transformed) and are round to whole numbers with the exception of omnivore and predator data on 29 August. Means in a row followed by same letter(s) are not different according to Waller–Duncan k-ratio (k = 100) t-test based on log (x + 1) transformation value

S + CP, S > MB. Abundance of *Meloidogyne* increased at the end of the pepper crop, and was highest in C and S and least in MB ($P \leq 0.05$). At the end of the cropping season in 2004, very low abundance of herbivores, omnivores and predatory nematodes occurred (Table 2).

Impacts on nematode community indices

In comparison with the C, all summer soil treatments resulted in a reduction in F/(F + B) for Pi in 2003 ($P \leq 0.05$), but not in 2004 (Fig. 2a, b). Although effects of soil treatments on F/(F + B) for Pf were different in both years, plots with MB always had the lowest F/(F + B). Nematode richness for Pi was suppressed in MB, S and S + CP in 2003 but was only decreased in MB and S in 2004 ($P \leq 0.05$, Fig. 2c, d). Richness for Pf remained lowest in MB in both years, whereas that in S and S + CP recovered to levels not different from CP (Fig. 2c, d).

Structure indices for Pi and Pf were both affected by treatment (Fig. 2e, f), where SI at Pf was lowest in the MB treatment in both years. The SI for Pi was increased by CP in 2003, but the

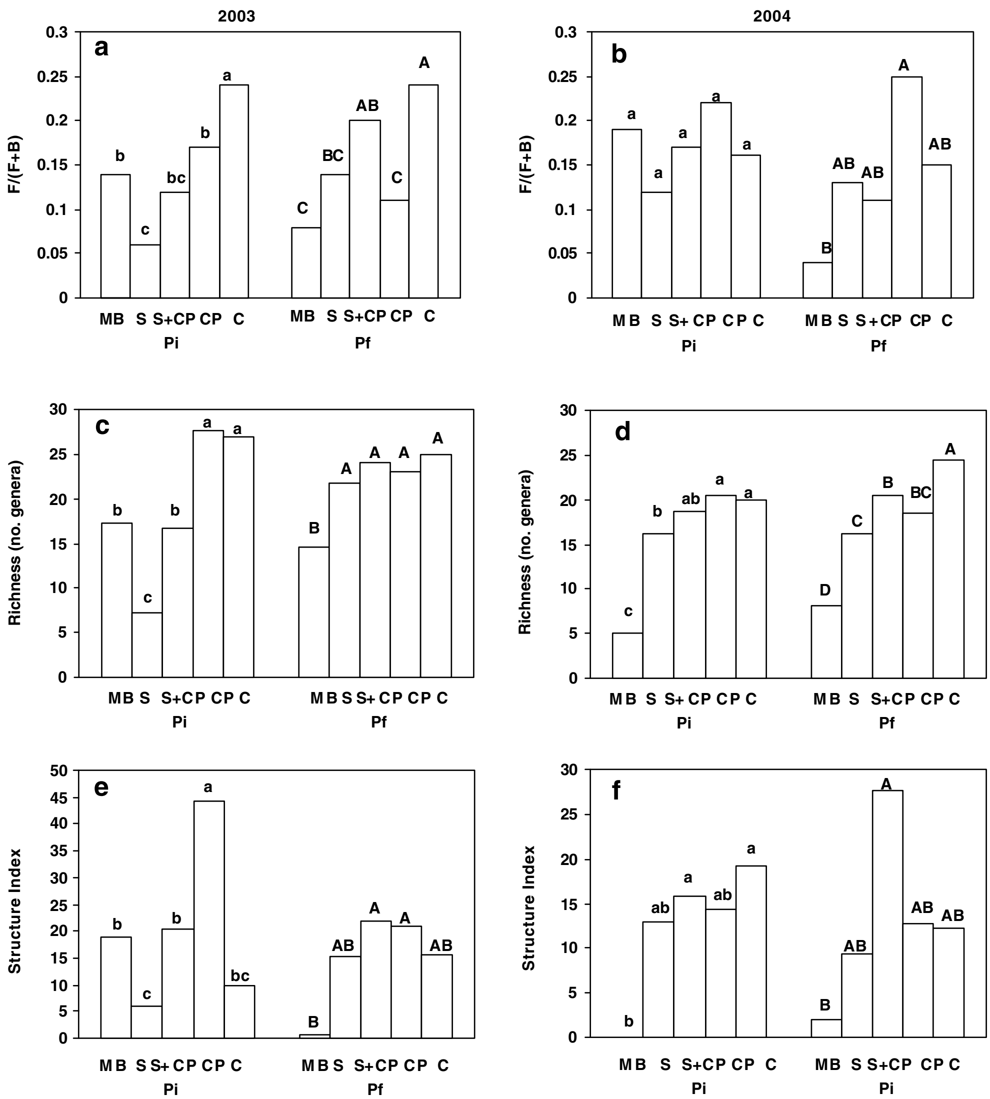

Fig. 2 Effects of pre-plant soil treatments on fungivore to total decomposer ratio [F/(F + B)], nematode richness, and structure index at the beginning (Pi) and the end (Pf) of pepper crop in 2003 and 2004. Treatment codes: MB = methyl bromide, S = solarization, S + CP = solarization + cowpea, CP = cowpea, C = control. Values are arithmetic means of four replications. Means with the same letter(s) within a sampling date (Pi or Pf) are not different according to Waller–Duncan *k*-ratio (k = 100) *t*-test

SI in CP plots was not different from C on other sampling dates (Fig. 2e, f). The lowest SI occurred in MB on three of the four sampling dates.

Impacts on other soil organisms

Methyl bromide and S, but not CP and S + CP, suppressed the Pf of enchytraeid worms relative to C on all sampling dates except of 2004 (Tables 1 and 2). At the final sampling of 2004, *Meloidogyne* juveniles parasitized at the cephalic region by *Drechmeria*-like nematode-endoparasitic fungi were observed (Table 2). The C had greater Pf of *Meloidogyne* parasitized by *Drechmeria*-like spores than CP, S + CP, and MB in 2004, coincident with the abundance of *Meloidogyne*.

Discussion

General impact of soil treatments on nematode communities

Weed fallow control is sometimes used to restore unbalanced soil properties in neo-tropical, low input cropping systems. However, the restoration of nematode community structure from fallowing depends on the length of the fallow period (Villenave et al. 2001). Although the fallow period for C was rather short (approximately 15 weeks) in the current experiments, it is anticipated to have less perturbation as compared to the toxicity from methyl bromide, heat from solarization, or the soil cultivation and nutrient enrichment from a cover cropping system. Results at Pi in 2003 fit this hypothesis better than those in 2004. In general, responses of nematode communities to soil treatments were more obvious at pepper crop planting soon after the summer treatments (Pi) than 4 months later at the end of the crop cycle (Pf). In 2003, total abundance of bacterivores and fungivores followed the hypothesized pattern, in which MB, S, and S + CP had greater impact on the community compared to C and CP. However, this perturbation did not persist after a cycle of vigorous growth of the pepper crop in 2003, except for the MB treatment on Pf of fungivorous nematodes. As demonstrated by Villenave et al. (2001), cultivation rapidly disturbs the nematode community structure restored by long-term fallow. Reduction of Pf of fungivores by MB indicates that this fumigant had relatively more persistent impact on fungivores as compared to the other soil treatments tested.

The impact of MB, S, and S + CP treatments on the abundance of omnivorous nematodes was delayed, with no difference from C at initial sampling, although CP enhanced this group of nematodes significantly. This enhancement by CP was similar to results obtained in plots amended with residues from another leguminous cover crop, *Crotalaria juncea* L. (Wang et al. 2003b). Impact of soil treatments on predatory nematodes would have followed the anticipated perturbation pattern if not due to the presence of *Seinura*, an aphlenchoid that can attack nematodes with larger body size than its own, compensating for its small size by paralyzing prey almost instantly when the spear is inserted (Thorne 1961). It is interesting that *Seinura* was found to be tolerant of the heat generated by solarization, unlike *Mylodiscus*, that was the dominant predators in other treatments, but did not survive in S plots.

The nematode community indices, SI, F/(F + B), and richness, were sensitive in detecting differences among the soil treatments at the end of both experiments. The consistency of SI is due to the sensitive and consistent response of nematode persisters (particularly omnivores) to soil perturbation. Bongers and Bongers (1998) considered omnivores and predators to be sensitive to disturbance, and weighted the calculation of their maturity index (MI) to reflect this, but MI was not sensitive to the soil treatments applied here (data not shown). The calculation of MI is greatly affected by the abundance of colonizing nematodes (Bongers and Bongers 1998). The calculation of SI places more emphasis on persisters than colonizers (Ferris et al. 2001), and was therefore a more sensitive index in our study. Forge et al. (2003) also found SI to be most sensitive to soil amendment treatments. Although the patterns of richness for Pf were not the same in 2003 and 2004, similar trends were observed. Soil communities with higher richness indicated a healthier soil (Doran et al. 1996; Wang and

McSorley 2005). Thus, richness is also a good indicator for these soil perturbations. Although F/(F + B) could detect differences among the soil treatment at the end of the pepper crop of both years, inconsistent trends were observed for CP treatment. This is most likely due to the very severe fungal disease outbreak in the CP treatment in 2004 (Saha et al. 2005), which resulted in a higher proportion of fungivorous nematodes, indicating more fungal decomposition pathway was taking place.

Inconsistent results between 2003 and 2004

Although weather conditions in the two seasons (2003 and 2004) were very different, overall effects of soil treatments on nematode community structure were fairly similar in both seasons, especially at Pf. One difference in results from 2004 compared to 2003 was that the C treatment did not support the greatest Pi of free-living nematodes in 2004. We propose that two factors may have contributed to the differences observed in 2004. The first factor was the application of glyphosate during the summer of 2004 in MB and C to reduce the weed biomass present in these treatments. While toxicity of glyphosate on soil nematodes was not examined, changes in the rhizosphere fungi due to application of glyphosate has been suggested (Huber et al. 2005; Kremer 2001). Similar changes in the soil environment might have affected the nematode communities as well. However, the great reduction in weed biomass in MB and C plots should have resulted in much less soil organic matter incorporated into soil prior to initial sampling in 2004 than in 2003, and thus probably reduced the microorganisms that could have supported more bacterivorous, fungivorous, omnivorous, and predatory nematodes in the soil.

The potential disturbance from weed management on nematode communities did not persist 4 months after pepper planting. In fact, the data here as well as that by Forge et al. (2003) and Yeates et al. (1999) revealed that nematode diversity is greater under herbicide-based management than under organic management. The abundance of fungivorous nematodes, F/(F + B), and richness for Pf of 2004 followed the hypothesized perturbation trend. Maintaining a great abundance of weed biomass in the MB plots in 2003 might have interfered with and reduced the impact of MB to the nematode communities. Conversely, application of glyphosate in 2004 reduced weed pressure in MB-treated plots, and resulted in a more severe impact of MB on total nematode and bacterivore numbers at Pi compared to either one of the solarization treatments (S or S + CP).

A second factor that might have caused differences in the results in 2004 was a disease outbreak on peppers following two hurricanes at the experimental site in 2004 (Saha et al. 2005). Pepper plants were severely stunted. In general, Pf of all nematode trophic groups were reduced in 2004 compared to 2003. However, these reductions in nematode numbers did not affect the pattern of perturbation of MB relative to the other treatments, based on several nematode community indices (SI, richness, and F/F + B).

Impact from MB

The current study documented the obvious negative impact of MB on nematode communities, and this impact lasted at least for one pepper cropping cycle except for the abundance of bacterivorous nematodes in 2003. We observed a different level of impact from MB in both years, with 2004 more severe than that in 2003, due to the weed management impacts discussed previously. This result is similar to a report by Yeates et al. (1991) in which methyl bromide eliminated nematode fauna, but nematodes, mainly Rhabditidae, began to recolonize in about one month. However, in around 5–6 months, nematode numbers were still lower in fumigated than in untreated soils (Yeates et al. 1991). This result is similar to ours in 2004 at the end of pepper crop cycle when toxicity of MB was not affected by residues of overgrown weeds as occurring in 2003. Although recolonization of nematodes can occur under certain post-treatment environments over a long-term, Yeates and van der Meulen (1996) reported that nematodes often failed to recolonize 52 months after MB treatment.

Response of nematodes to toxic compounds has been shown to be genus or species specific instead of generalized among a trophic group. For example, Lau et al. (1997) found that the bacterial-feeding nematode, *Cruznema tripartitum*, provided a useful bioassay for the presence of several biologically active toxicants. In the current experiment, no particular nematode genus showed rapid resurgence after fumigation, but *Acrobeles* was always reduced in the MB plots throughout the experiment as compared to the C, indicating a genus sensitive to this disturbance.

Impact of solarization

When sufficient heat is achieved during solarization, many species of plant-parasitic nematodes can be suppressed by solarization for at least one cropping season (Chellemi et al. 1993; McSorley and Parrado 1986; Overman 1985). Studies by Heald and Robinson (1987) suggested that daily exposures of *Rotylenchulus reniformis*-infested soil to 42.5°C for sublethal time periods had a cumulative lethal effect. While the lethal temperature for *M. incognita*, the most important plant-parasitic nematode of pepper plants at this field site, is yet to be determined, a preliminary laboratory experiment indicated that juveniles of this species were killed after an exposure time in water of 15 h at 42°C (Wang K-H, unpublished). Therefore, number of days with maximum temperature above 42°C was monitored in the experiment. Overall average temperatures (33°C) and number of days with maximum temperature above 42°C were similar between the two solarization treatments, indicating that adding the cowpea residues into the solarization treatment did not generate more heat than S alone. However, recovery of root-knot nematodes after one cycle of pepper crop revealed that S + CP could suppress root-knot nematodes to a level equivalent to that achieved by MB in both years, whereas S alone could not. Enhancement of natural enemies of root-knot nematodes in S + CP compared to S could be an explanation. Many soil antagonists of plant pests, such as *Bacillus*, *Pseudomonas*, and *Trichoderma* can survive solarization, or can rapidly colonize the soil substrate made available following treatment (Katan 1987; Stapleton and DeVay 1995). However, isolation of selected beneficial rhizosphere bacterial populations including Gram +ve bacteria, fluorescent pseudomonads, and siderophore producing bacteria at this site indicated that no treatment consistently enhanced populations of these organisms (Kokalis-Burelle et al. unpublished). A nematode-endoparasitic fungus resembling *Drechmeria* sp. was detected parasitizing root-knot nematodes at final sampling of 2004. However, the incidence of parasitism followed the pattern of root-knot population densities rather than root-knot nematode suppressiveness.

Impacts from S on nematode communities were only short-term. Nematode abundance and community indices recovered to levels not different from the control at the termination of pepper crop. These data thus support the speculation that free-living nematodes are more likely than plant parasites to survive solarization, and recolonize the soil after treatment (Katan 1987; Stapleton and DeVay 1995).

Impact of cowpea cover cropping

Although 'Iron Clay' cowpea was known to be a poor host to *M. incognita*, it did not have allelopathic effects in suppressing nematodes after incorporation into the soil (Wang et al. 2003a). In the current study, the CP treatment did not suppress the population densities of *Meloidogyne* spp. after a susceptible crop such as pepper was planted, similar to results reported earlier (Wang et al. 2003a). In 2004 during an outbreak of a *Pythium* disease, the organic matter input from CP increased the disease incidence (Saha et al. 2005). On the other hand, when such a disease epidemic is not a factor, enhancement of soil health by cover cropping is encouraging, as seen from the increased levels of bacterivores, fungivores, omnivores, and predators, and high values of richness and SI in the CP treatment.

Combination of solarization and cowpea cover crop

While CP and S may have disadvantages by themselves, results from this experiment supported the hypothesis that integrating the CP treatment with solarization could improve the suppression of herbivores better than CP alone, and reduce the impact generated by solarization alone. With the combination of S + CP, herbivores were suppressed relative to CP alone at Pf of 2003, and relative to solarization alone at Pf of 2004. The combination of S + CP also achieved the level of suppression by MB at Pf in both years, which was not achieved by either S or CP alone. Impact generated by S (based on low SI) at Pf was not different from MB in both years, but that by S + CP was consistently less (based on higher SI) than MB in both years.

Conclusion

Impact from soil treatment based on nematode community studies in general followed the hypothesized trend of MB > S > S + CP > CP > C. Omnivorous nematodes were the most sensitive nematode trophic group, with impact from soil treatment lasting until the end of the pepper crop in both years. Despite rather different conditions during the 2 years, nematode community indices F/(F + B), richness, and SI response rather consistently to these soil perturbations. While disturbance from MB on the nematode communities lasted at least until the end of the subsequent pepper crop, that from the solarization often disappeared after pepper planting. Growing a cover crop of CP enhanced many of the beneficial nematodes involved in nutrient cycling but failed to reduce the population densities of herbivorous nematodes at pepper harvest. However, combining CP + S reduced the impact from S alone on nematode communities, while achieving a suppression of *Meloidogyne* spp. equivalent to MB at crop harvest in both years. In addition to the experimental soil treatments, application of glyphosate, and a disease epidemic following hurricanes in 2004 acted as additional sources of impact to nematode communities, yet disturbance of MB to nematode community structure was consistent in both years.

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